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HOMOLOGIES OF THE EXCRETORY SYSTEM OF THE FORKED-TAILED CERCARIAE

A PRELIMINARY REPORT *

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Very little is known of the homologies of the protonephridial system in the various subdivisions of the Trematoda. Most of the anatomical studies on this group have been made from toto mounts and serial sections of preserved material, in which locating the flame cells and tracing the finer branches of the excretory system is practically impossible. My work has convinced me that a more complete knowledge of this system will do much to clear up relationships and to establish natural families. Also an increased knowledge of the excretory systems of little known types of cercariae will be of great help in solving life-histories by suggesting the groups of adults to which such forms belong. In certain cases the close relationship of two cercariae may be shown by comparisons of their excretory systems, when on account of differing degrees of development of adaptive larval characters they superficially appear to be very different.

The work on larval trematodes of which this paper forms the first published part was carried on at the University of Michigan Biological Station at Douglas Lake, Michigan, during the summers of 1914, 1915, and 1916. The region around Douglas Lake is very favorable for work on these forms since an abundance of material of a large variety of trematodes is readily available. I wish to express my appreciation to the University of Michigan Biological Station for facilities provided for carrying on this work. Thanks are due Mr. H. B. Baker for the identification of the molluscan hosts.

The best results in tracing the excretory systems of larval trematodes can be obtained from high power studies on living animals. To make such work effective it is important to have an abundance of material. By using thin cover glasses and slowly removing the water from the preparation even cercariae so small that they are almost invisible to

* Publication from the University of Michigan Biological Station.

the naked eye can be slowed down and flattened so that they can be studied under the oil immersion. Just before a cercaria goes to pieces from drying and flattening the movements of the flame cells are accentuated and the smaller tubules distended so that they become clearly visible. The use of large numbers of preparations, which is easily possible on account of the great numbers of cercariae in one infected snail, will gradually reveal the number and position of the flame cells and the pattern of the tubules. Larger agamodistomes* and adults can be mounted in a ring of vaselin, somewhat compressed and studied living for several hours or even a whole day. Fully developed cercariae should be mounted for this kind of study in pond water and agamodistomes and adults in normal saline. Aside from the excretory system much valuable data on the methods of locomotion, movements, and changes in shape, can be gained only from the study of the living animal. In fact in most cercariae it is possible to work out the structure much more completely in living than in preserved material. Looss (1894: 3) very strongly advocates the use of living animals in the study of trematodes and much of his most important morphological work on this group was accomplished by this method. La Rue (1917: 5) in a recent paper in which he describes two agamodistomes from snakes makes an appeal for the use of better and more varied staining methods in the study of parasitic worms. I would add to this a strong plea for more study of the living animals especially when dealing with cercariae, agamodistomes, or small adult trematodes. Much unsatisfactory work and many errors can be avoided by the adoption of these two improvements in methods of work.

The present paper consists of a comparison of the excretory systems of five forked-tailed cercariae, of which two, *Cercaria douthitti* Cort and the cercaria of *Schistosoma japonicum,* are already known and the others are new species. *Cercaria douthitti* was described from *Lymnaea reflexa* Say from the vicinity of Chicago, Illinois (Cort, 1915: 49), but at that time only a part of the excretory system was worked out. The cercaria of *Schistosoma japonicum* has been described by several Japanese workers but its anatomy has not been adequately worked out. In this connection I describe only the excretory system of this cercaria since a detailed account of its anatomy will appear in the near future in the Zoological Series of the University of California Publications. My material of the cercaria of *Schistosoma japonicum* was obtained from infected snails sent to Professor C. A. Kofoid from Japan by Professor A. Fujinami of the University of Kyoto. To both of these gentlemen thanks are due for making possible my studies on this

* The term agamodistome (from Agamodistomum Stossich 1892) I accept for larval trematodes when known only in the encysted or "resting stage."

species. The three new cercariae are from the Douglas Lake region. One of these, a very large form from *Planorbis trivolvis* Say, I name *Cercaria elephantis* from its large size and from the fact that its body when seen from side view after the loss of its tail resembles an elephant's head. The second of the new forms was found in *Lymnaea emarginata angulata* Sowerby and is given the name *Cercaria emarginatae* and the third from *Physa ancillaria* Say is called *Cercaria douglasi* from Douglas Lake. These three species and several others of the forked-tailed cercariae not included here will be described in a later publication. Recently the forked-tailed cercariae have been brought into prominence by the work of Leiper and others on the life-histories of the human schistosomes, so that it becomes very important that this group should be carefully worked up.

There has been a tendency since the discovery of the life-histories of the human schistosomes to relate all forked-tailed cercariae to this group without making careful analysis. Faust (1917: 119) in a description of two forked-tailed cercariae makes the following statement: "This group of larval trematodes (the forked-tailed cercariae) is characterized by a forked tail and as far as the writer knows, the absence of a true pharynx. However, glands of the pharyngeal region may lead one to consider the mass a pharynx, which is evidently the error Looss (1896) made in the study of *Cercaria vivax* Sons." Looss' figures of both immature and mature specimens of *Cercaria vivax* (Looss, 1896, pl. xv, figs. 174-176) show the structure of the pharynx so clearly outlined that it seems impossible he could have erred in this particular. Now my discovery of other forked-tailed forms with pharynges establishes this as a definite group of the forked-tailed cercariae and shows that within this group, which my observations on the excretory system indicate to be a natural one, there are represented two different families.

Cercaria douthitti Cort 1914

In the summers of 1915 and 1916 *Cercaria douthitti* was found in the region of Douglas Lake, Michigan, in *Lymnaea stagnalis appressa* Say and *Lymnaea stagnalis perampla* Walker. Besides the completion of the study of the excretory system there are several points which should be added to my original description of this species. Careful studies of living specimens show the outlines of the esophagus and the intestinal ceca as far as the acetabulum. Whether they end here or are merely masked in the posterior region by the mass of glands could not certainly be determined. It was also found that the whole surface of the body and tail is evenly covered with very minute spines which are visible only with the highest power of the microscope. Also the number of cephalic glands is ten instead of eight.

The excretory bladder of *Cercaria douthitti* (Fig. 1, *b, tb*) extends the length of the tail and divides to open at the tips of its bifurcations. At the base of the tail where the bladder passes from the body into the tail the fused nature is indicated by a small island (*i*). The part of the bladder in the body proper (*b*) which will remain after the loss of the tail as the bladder of the adult is V-shaped. The sides of the V extend up to the anterior margin of the acetabulum and turn backward to points (*p*) near the sides of the body at the level of the posterior margin of the acetabulum, where they receive the anterior and posterior collecting tubes (*act, pct*). A short region of the bladder on each side near the points where the collecting tubes enter is ciliated. The anterior collecting tube receives capillaries from three flame cells, one at the level of the posterior margin of the oral sucker, the second at the level of the eye-spots, and the third at about the level of the anterior margin of the acetabulum (*ff*). The posterior collecting tube on each side also receives three capillaries, two from flame cells in the postacetabular region and the third from a very large flame cell in the anterior region of the tail. The character of these flame cells is shown in Figure 2*D*. This is the type of flame cell found in all of the forked-tailed cercariae studied. The flame cells and tubules of the body region are limited to narrow areas at the sides and do not invade the central core of the body which is crowded full of unicellular glands (Cort, 1915, Figs. 55, 56).

The Cercaria of *Schistosoma japonicum*

The excretory system of the cercaria of *Schistosoma japonicum* is shown in Figure 2*A*. The bladder corresponds to that of *Cercaria douthitti* except that it extends further in front of the acetabulum. The anterior and posterior collecting tubes show distinctly greater caliber than the capillaries. The anterior collecting tube receives two capillaries on each side from flame cells in the preacetabular region and the corresponding posterior collecting tube also receives two capillaries, one from a flame cell near the posterior end of the body, and the other from one in the anterior region of the tail. In all there are six flame cells in the body arranged along the sides and two in the anterior region of the tail. A comparison of this type of system with that of *Cercaria douthitti* shows that they are homologous except for the number of flame cells.

Cercaria elephantis nov. spec.

Forked-tailed cercaria without pharynx; eyespots present; divided lobes of tail less than half length of main stem and constricted off from it; body and tail including lobes covered with minute spines, evenly dis-

tributed; excretory system with V-shaped bladder, ten flame cells in body and two in tail, openings of bladder at tips of divided lobes; between fifty and sixty cephalic glands which distend posterior part of body; body 0.16 mm., stem of tail 0.59 mm., lobes of tail 0.11 mm. in length; in digestive gland of *Planorbis trivolvis* Say from Douglas Lake, Michigan.

The excretory system of *Cercaria elephantis* corresponds exactly to that of *Cercaria douthitti,* having the same number of flame cells in relatively the same position, the same type of bladder with its openings at the tips of the divided lobes of the tail and even the little island (Fig. 1 *i*) in the same position at the base of the tail. The portion of the bladder in the main stem of the tail is of course longer than in the former species on account of the greater length of the tail. In fact, with this one variation the drawing of this system in *Cercaria douthitti* would do equally well for *Cercaria elephantis.*

Cercaria emarginatae nov. spec.

Forked-tailed cercaria with pharynx and without eye-spots; lobes of tail almost as long as stem and not constricted off from it; number of cephalic glands six, extending into postacetabular region; heaviest spination over anterior tip and around acetabulum, with rest of body only sparsely covered; intestinal ceca extend almost to posterior end of body; excretory bladder V-shaped, ten flame cells in body and four about in mid region of stem of tail; openings of bladder at sides of divided lobes of tail; body 0.16 mm., stem of tail 0.23 mm., lobes of tail 0.20 mm. in length; in digestive gland of *Lymnaea emarginata angulata* Sowerby from Douglas Lake, Michigan.

The excretory system of *Cercaria emarginatae* is shown diagrammatically in Figure 2 *B*. The excretory bladder corresponds to that of *Cercaria douthitti* except that the openings are at the sides of the divided lobes of the tail. The number of flame cells in the body of this cercaria is ten, arranged along the sides as in the other forms. In the tail there are four flame cells, two on a side, located about the middle of the stem and connected with the posterior collecting tube of the body by a long tubule on each side. A form closely related to *Cercaria emarginatae* was worked out during this past summer by one of my students, Mr. John C. Johnson. The relations of the excretory system in this species correspond to those in *Cercaria emarginatae* except for the position of the flame cells in the tail which was the same as in *Cercaria douglasi,* and for the island at the base of the tail.

Cercaria douglasi nov. spec.

Forked-tailed cercaria with pharynx and no eye-spots; lobes of tail more than half length of main stem and not constricted off from it;

heavy spination over anterior tip and around ventral sucker; scattered spines over rest of body; cephalic glands four, not extending into post-acetabular region; excretory bladder with commissure in front of acetabulum connecting branches; flame cells as in *Cercaria emarginatae* except that those of tail are in its anterior portion; intestinal ceca extend two-thirds of distance between acetabulum and posterior end of body; body 0.14 mm., stem of tail 0.18 mm., divided lobes 0.16 mm. in length; in digestive gland of *Physa ancillaria* Say from the Douglas Lake region.

The excretory system of *Cercaria douglasi* is shown in Figure 2 *C*. The bladder is quite different from that of *Cercaria emarginatae,* since the sides of what constitutes the V in that species are in *Cercaria douglasi* united by a commissure which makes a triangle with the base in front of the acetabulum. The anterior and posterior collecting tubes on each side enter the bladder at the angles of the base of the triangle. The number of flame cells and their general arrangement is the same as in *Cercaria emarginatae* except for the position of the flame cells of the tail.

GENERAL DISCUSSION

An analysis of the forked-tailed cercariae described above shows that they fall into three distinct groups. The first group might be characterized by the absence of a pharynx, by the fact that the lobes of the tail are less than half the length of the main stem and definitely constricted off from it and by the presence of eye-spots. This group includes of my material *Cercaria douthitti* and *Cercaria elephantis*. The second group, the cercariae of the human schistosomes, is represented by the cercaria of *Schistosomum japonicum*. This group agrees with the first in characters one and two, but has no eye-spots. Group three might be characterized by the presence of a pharynx and the fact that the lobes of the tail are almost as long as the stem and not constricted off from it. The first two groups belong to the family Schistosomidae, but the third group differs from this family in the presence of a pharynx.

A comparison of the excretory systems of these five cercariae shows a remarkable uniformity. The exact correspondence between this system in *Cercaria douthitti* and *Cercaria elephantis* would seem to indicate close relationship and if the adults were known I should expect to find them belonging to the same genus or closely related genera. Here is a case where cell constancy indicated by a correspondence in number of flame cells is carried beyond the species limit. One would hardly expect to find specific differences in the excretory systems of trematodes belonging to the same genus except those produced by differences in size relations. The constancy of the excretory systems

of these two cercariae is all the more striking when their superficial differences are taken into consideration. *Cercaria elephantis* has a tail almost three times as large as that of *Cercaria douthitti* and a very much larger number of cephalic glands. The eye-spots also are much larger in the former species.

A comparison of the type of excretory system found in the cercaria of *Schistosoma japonicum* with the conditions in the first group (Figs. 1 and 2 *A*) shows that they are homologous except for the number of

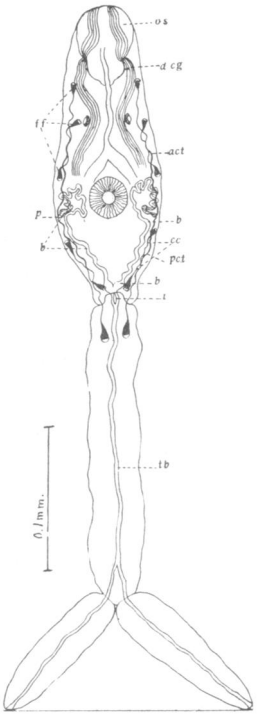

Fig. 1.—*Cercaria douthitti,* ventral view, to show excretory system. Cephalic glands not shown. *act,* anterior collecting tube; *b,* bladder in body region; *cc,* capillaries; *dcg,* ducts of the cephalic glands; *i,* island in excretory bladder; *os,* oral sucker; *p,* point where collecting tubes join bladder; *pct,* posterior collecting tube; *tb,* extension of bladder into main stem of tail.

flame cells. The cercaria of *Schistosoma japonicum* has the smallest number of flame cells that I have ever observed in a fully developed cercaria or seen recorded in the literature.

More striking still is a comparison between these first two groups and the conditions found in the excretory system of the third group (cf. Fig. 2 *B* and *C*). The forms belonging to this group have a distinct pharynx, which sets them off very clearly from the first two groups and places them outside the family Schistosomidae. Yet com-

parisons of the excretory systems show striking homologies which must certainly indicate a fairly close relationship between the family to which these forms belong and the schistosomes. Therefore, the knowledge of the life-history of a member of this group such as *Cercaria emarginatae* would help us to understand the relations of the family Schistosomidae to the other digenetic trematodes.

Cercaria vivax Sonsino belongs to the third group. Looss (1896: 210) describes this species fully, but does not show the excretory system sufficiently for the determination of its homologies. He shows six flame cells in the tail, but does not make clear their connections. His

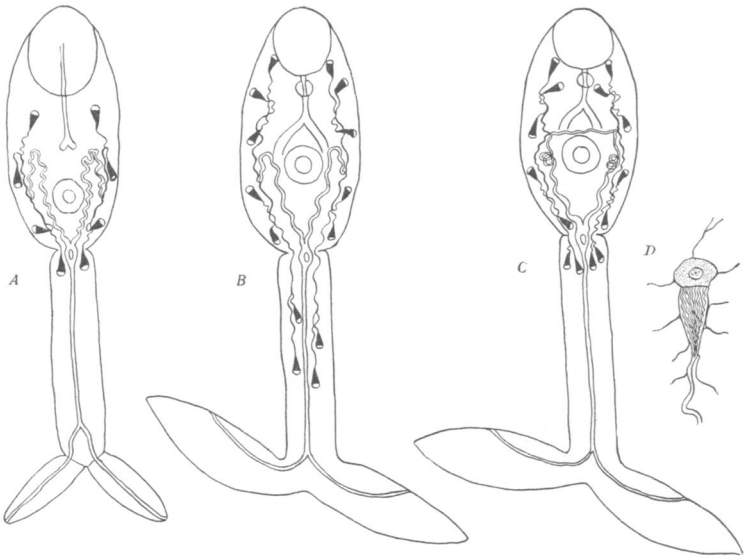

Fig. 2.—Diagrams of the excretory systems of three different forked-tailed cercariae. *A,* Cercaria of *Schistosoma japonicum. B. Cercaria emarginatae. C, Cercaria douglasi. D,* Typical flame cell of the forked-tailed cercariae. Very highly magnified.

work on the development of this form (Looss, 1896, Pl. xv, Figs. 172, 173) indicates very clearly the double origin of the type of excretory system found in the forked-tailed cercariae. This is suggested in the mature cercariae described above by the complete separation of the flame cells of each side, the division of the bladder in the body, the island at the base of the tail and the division of the bladder to open on the lobes of the tail.

The fundamental homology of the excretory systems of these forked-tailed cercariae indicate that at least in this group the pattern of the excretory system is very conservative. I have in addition a considerable number of unpublished observations on the excretory

systems of the cercariae of other groups of trematodes which supports this view, and tend to extend the principle of conservativeness to other trematode groups. This indicates that studies on the excretory systems of cercariae may go far in establishing the true relationships between the various subdivisions of the digenetic trematodes.

SUMMARY

The excretory system was carefully studied in five forked-tailed cercariae, *C. douthitti* Cort, the cercaria of *Schistosoma japonicum*, *C. elephantis* n. sp., *C. emarginatae* n. sp., and *C. douglasi*. Altho these five fall into three separate groups which represent at least two distinct families, this system shows remarkable uniformity.

In *C. douthitti* and *C. elephantis* the system corresponds both in the arrangement of tubules and in the number of flame-cells, suggesting close relationship for these species.

The excretory system of the cercaria of *Schistosoma japonicum* is the simplest known in a fully developed cercaria and has the fewest flame-cells.

Cercaria douglasi and *C. emarginatae* differ considerably from the other three forms studied. In the presence of pharynges, also, they depart from conditions in the family Schistosomatidae. The similarity of the excretory system, however, demonstrates their relationship to that family.

These observations indicate the conservatism of the excretory system in trematodes and its value in establishing relationships in this group.

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